

TROPHIC GROUP AND EVOLUTION IN BIVALVE MOLLUSCS

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ABSTRACT. Deposit-feeding marine benthic invertebrates ingest sediments and feed principally upon bacteria, whereas suspension-feeders feed mainly upon phytoplankton. This distinction is important because the predictability of phytoplankton is less than that of within-sediment bacteria. As a result, suspension-feeding populations fluctuate more than deposit-feeding populations. Possible consequences of these differences include: (1) The evolutionary turnover of deposit-feeding groups should be less than that of suspension-feeders. (2) Being more subject to environmental perturbations, the longevity of suspension-feeding genera should be less than that of deposit-feeding genera, and (3) trophic structure of deposit-feeding communities should be conservative, with few changes in trophic structure since the early development of the adaptive zone. Preliminary evidence from the fossil record supports these predictions. (i) Bretsky's interpretation of Palaeozoic community evolution, as being the result of nearshore-offshore differences in environmental predictability can be shown to be strongly influenced by trophic group. (ii) If survivorship curves are constructed for genera of bivalve superfamilies, the following mortality rates obtain for genera: Nuculoida (deposit-feeder)—0.8%/million years, Pectinacea (suspension-feeder)—1.2%/my, Pteriacea (suspension-feeder)—1.5%/my, Veneracea (suspension-feeder)—1.5%/my. Clearly suspension-feeding bivalve genera were shorter-lived. (iii) Finally, Levinton and Bambach have shown a similarity in the ecology of Silurian and Recent deposit-feeding bivalve mollusc communities.

IN recent years many palaeoecologists have attempted to make evolutionary predictions from ecological premises. A prediction following from ecological arguments is the statement 'We contend that the genetic-adaptive strategy employed by a species population depends in large part on the regularity, direction, and rate of change in environmental stability' (Bretsky and Lorenz 1970, p. 2449). This and other contributions have speculated on the causes of major evolutionary events, such as adaptive radiations (e.g. Valentine 1968; Bretsky 1969; McAlester 1970). It is in this spirit that I present some ideas on the evolutionary consequences of different trophic adaptations.

Most marine benthic invertebrates belong to one or the other of two main feeding types: *deposit-feeders* and *suspension-feeders*. Deposit-feeders are those forms that ingest sediments, whereas suspension-feeders feed by straining food out of sea-water. Many species cannot be easily classified into one feeding type or the other. For example, the mastracean bivalve, *Mulinia lateralis*, has a typical suspension-feeding siphon and ctenidia apparatus, but often feeds on food that is resuspended from bottom sediments. Some other species show distinct behavioural switch mechanisms from deposit-feeding to suspension-feeding (e.g. tellinacean bivalves—Brafeld and Newell 1961). However, most taxa can be primarily assigned to either the deposit-feeding or suspension-feeding trophic group.

In this paper, it is contended that these two trophic groups live under distinctly different regimes of food predictability. The suspension-feeding group is regarded as living with highly unpredictable food supplies, while the deposit-feeders have stable food supplies. This leads to differences in ecological interactions between species. It also implies that the evolutionary history of suspension-feeders should be more erratic than that of deposit-feeders.

DIFFERENCES BETWEEN DEPOSIT-FEEDERS AND SUSPENSION-FEEDERS

In a recent paper, Levinton (1972*a*) discussed in detail the major ecological differences between the deposit-feeding and suspension-feeding trophic groups. In summary, suspension-feeding species largely depend upon phytoplankton for their food supply. The abundance of this food supply is variable in both time and space. The phenomena of phytoplankton blooms, control of patchiness by currents and water-mixing effects, and seasonal succession of phytoplankton species, creates an essentially unpredictable food supply for benthic suspension-feeders which, being fixed upon the bottom, depend upon whatever happens to be in the immediately overlying water. As a result, suspension-feeders tend to have patchy spatial distributions, and spatially non-random source of mortality (Connell 1955, 1963). The abundance of suspension-feeders may fluctuate strongly over time (Savage 1956; Coe 1953; Levinton 1970; Trevallion, Edwards and Steele 1970). The maximum abundance of suspension-feeders is correlated with parameters related to the optimal physical characteristics of the sediment-water interface, such as its physical stability, and to the lack of bottom mobility of sedimentary grains (Rhoads and Young 1970; Sanders 1958). Suspension-feeders are probably not most abundant where potential food is greatest in abundance (Rhoads 1973).

In contrast, most deposit-feeding benthic species depend upon bacteria as their proximal source of food (Fenchel 1970). Bacteria are very abundant in bottom sediments, particularly in muds (Zobell 1938). Unlike phytoplankton they show relatively modest seasonal changes in abundance, as do the organic detrital particles upon which they live (Longbottom 1968; Ockelman 1958). In addition, the abundance of bacteria in bottom sediments is controlled principally by properties of the sediments themselves, as opposed to the abundance of phytoplankton, which is controlled by the overlying water. Finally, the sediment reworking activities and faecal pellet formation of deposit-feeders dramatically homogenizes the sediment, further enhancing the uniformity of the environment of deposit-feeders (Rhoads and Young 1970; Levinton 1971; Rhoads and Stanley 1965). The mobility of deposit-feeders also permits complete choice among foods, and complete exploitation of a food source. The net result of this relatively predictable trophic network is a set of populations that are usually randomly or uniformly distributed in space (Connell 1963; Gilbert 1970; Levinton 1972*b*; Holme 1950). Deposit-feeders show uniformity in community composition and structure, abundance being related to parameters concerned with food availability (Sanders 1958, 1960; Levinton 1971; Newell 1965).

ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

The consequences of marked differences in predictability of food and energy have been discussed by Valentine (1971). Biomes with unpredictable nutrient supplies can be shown to have species with rapidly fluctuating populations, and little niche specialization. Sanders (1968) coined the terms 'physically controlled' and 'biologically accommodated' to characterize unstable and highly stable biotic environments, respectively. Although he used these terms to classify major habitat differences (i.e. shelf *v.* deep-sea), it is clear that within major biomes, such differences may still

be observed. Suspension-feeders and deposit-feeders often live under similar regimes of temperature and salinity fluctuation. However, they operate under totally different regimes of temporal and spatial variations of food supply. Suspension-feeders should therefore *not* participate in communities of species whose competitive interactions for food have resulted in niche specificity. This point is not generally accepted in the literature (see Walker 1972). In contrast, deposit-feeders can be expected to show competitive interactions for food with attendant specializations in diet and living position. These competitive interactions have been observed in many studies (Segerstrale 1960, 1962, 1965; Vasallo 1969; Levinton 1969, 1971; Rhoads and Young 1970; Mangum 1964; Sanders 1960). Few studies have ever demonstrated competitive interactions for food among suspension-feeders (but see Sanders *et al.* 1962; and Bradley and Cooke 1958 for an exception). Thus, it is concluded that with respect to food supply, deposit-feeding communities are largely controlled by biological interactions, whereas suspension-feeding communities are controlled by large-scale and unpredictable fluctuations in factors unrelated to interspecific interactions. This statement applies to competition for food.

The conservatism of deposit-feeding populations relative to the susceptibility to rapid change of suspension-feeding populations has some evolutionary consequences. Because deposit-feeders control their own substratum characteristics, are food-limited, and do not radically fluctuate in numbers over time, it is expected that the structure of these communities would be established very early in evolutionary time, with few subsequent basic changes. On the other hand, the variable nature of the food supply for suspension-feeders, plus the great changes in the plankton that have taken place during geologic time (Tappan 1972; Tappan and Loeblich 1971), suggest that suspension-feeding populations should have experienced many turnovers. This conclusion is superficially at odds with the hypothesis that biotic stability is maintained by environmental instability (Bretsky and Lorenz 1969). It is possible that, for a given trophic group, the effect of trophic stability is inherently different from that of variations in the physical aspects of the environment, such as temperature and salinity. Because they depend upon optimal characteristics of the overlying water for feeding, suspension-feeders are probably more susceptible to environmental change than deposit-feeders.

Some preliminary evidence suggests that the above predictions are at least consistent with observed patterns of evolution and extinction. The trophic structure of protobranch bivalve (deposit-feeding) communities in the Silurian of Nova Scotia is very similar to those of modern, bivalve-dominated deposit-feeding communities (Levinton and Bambach 1969; Levinton and Bambach, manuscript). Furthermore, Bretsky's (1969) characterization of biotic stability in Palaeozoic benthic communities can be reinterpreted in the light of the above arguments. Bretsky notes that offshore communities, inferred to have lived under physically stable conditions, have undergone several biotic turnovers. Nearshore communities living under unpredictable regimes, changed little. However, the offshore communities are dominated almost exclusively by suspension-feeders (brachiopods, ectoprocts, etc.). In addition, at times of biotic turnover in the offshore communities, the suspension-feeding aspects (brachiopods and epifaunal bivalve molluscs) of the onshore communities change as well (Bretsky 1969, p. 56). Thus we might reinterpret the onshore-offshore

distinction proposed by Bretsky as being rather the result of difference in trophic stability between deposit-feeders and suspension-feeders. Probably, the truth lies somewhere intermediate between these two hypotheses.

A final prediction follows from the above arguments. If we examine the fossil record, the relatively tenuous existence led by suspension-feeding taxa should result in their being shorter-lived, on the average. Thus, if we plot a survivorship curve for deposit-feeding genera, the rate of mortality should be less than that of related suspension-feeding groups. One need only have the length of life of all the individual genera. Having the distribution of life-spans, one can consider a group of genera as a cohort and plot the survivorship, as for a single species population (Levinton and Bambach 1970).

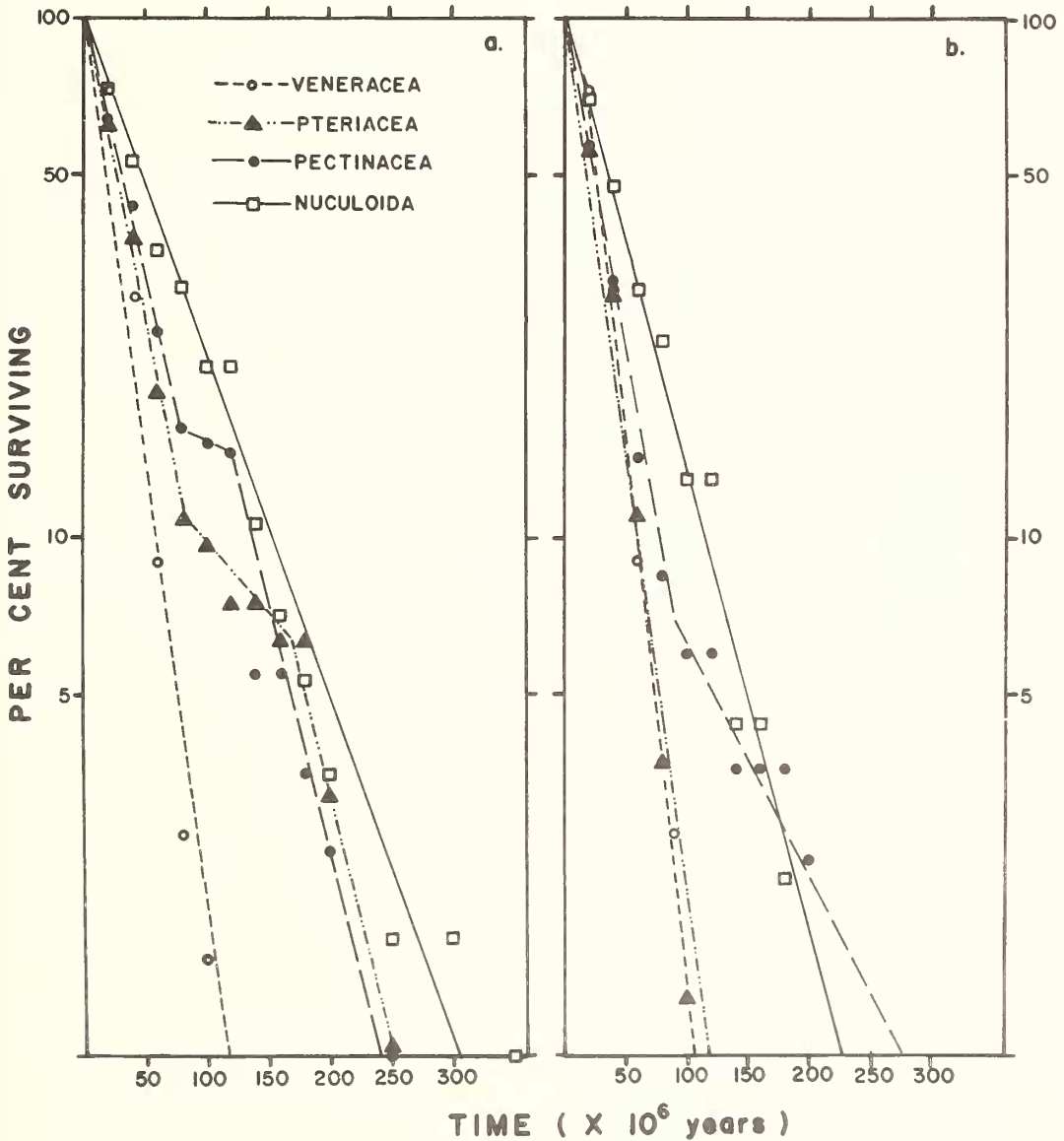
Bivalve molluscs of the order *Nuculoida* were selected as a homogeneous deposit-feeding group. Unfortunately, no other bivalve group can be regarded as strictly deposit-feeding. The *Tellinacea* have both deposit-feeding and suspension-feeding representatives, sometimes within even the same genus (Pohlo 1969). A further complication is that many *nuculoid* bivalves come from deep-water, confounding their deposit-feeding status with factors related to physical stability. Three suspension-feeding superfamilies, *Pteriacea*, *Pectinacea*, and *Veneracea*, were used for contrast. The first two have representatives back into the Palaeozoic, allowing a potentially parallel history to the *nuculoids*. The *Veneracea* have a more recent origin in the Lower Cretaceous. Data were compiled from the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1969). Genera with no fossil record were excluded from the analysis.

The results of the survivorship analysis are shown in text-fig. 1. The *nuculoids* show a constant rate of mortality which is lower than the maximum rates of mortality shown by the *Pteriacea* and the *Pectinacea*. The *Veneracea* also display constant mortality, though higher in rate than the *Nuculoida*. Therefore, it is concluded that the rate of mortality of suspension-feeding taxa is higher than that of deposit-feeders.

The survivorship curves for the *Pteriacea* and *Pectinacea* both show a notable break in slope, from high to low to high mortality (text-fig. 1*a*). The position of this break correlates with those taxa that are biogeographically cosmopolitan. Apparently, those *pteriacan* genera that originated in the Triassic produced a number of genera that were cosmopolitan and long-lived. In the case of the *pectens*, there were two major periods of cosmopolitan dominance: Carboniferous-Permian and Mesozoic. If we subtract those genera classified in the *Treatise* to be 'cosmopolitan', then these breaks in slope disappear from the survivorship curves almost entirely (text-fig. 1*b*). The lower rate of mortality still obtains for the *Nuculoida*, relative to the suspension-feeding groups.

It is concluded, therefore, that the ecological characteristics of different trophic groups can lead to differences in the pattern of evolution of these groups. These patterns can be observed in (1) the relatively low 'generic mortality rates' of deposit-feeders, relative to suspension-feeders, (2) the slower evolutionary turnover of deposit-feeding groups relative to suspension-feeding groups, and (3) the apparent tendency of some suspension-feeding groups to show periods of cosmopolitan appearances, perhaps correlated with global changes in the plankton (Tappan and Loeblich 1971). It has also been demonstrated that it is possible to partition bio-

geographic phenomena from other ecological factors, through the use of survivorship curves. This latter conclusion may be significant in our future analyses of the major factors controlling evolution.



TEXT-FIG. 1. Survivorship analysis of (1a) the Veneracea (96 genera), Pteriacea (94), Pectinacea (108), and Nuculoida (56). Fig. 1b indicates the curves obtained when cosmopolitan genera are omitted. From fig. 1b, mortality rates are (first 90% of survival): Veneracea—1.5%/million years, Pteriacea—1.5%/million years, Pectinacea—1.2%/million years, Nuculoida—0.8%/million years.

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